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# The large branchiopods (Crustacea: Branchiopoda) of gnammas (rock holes) in Australia

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## Abstract

Small water-filled hollows in exposed rock masses occur across Australia and are particularly common in south-western Australia on granite. Sixteen species of large branchiopods, comprising six anostracans, eight conchostracans and two notostracans occur in these gnammas, with at least *Branchinella longirostris, Limnadia badia* and *Caenestheriella maraie* in south-western Australia and *Limnadia urukhai* in south-eastern Queensland obligate inhabitants. In Western Australia five common species (the three above plus *Lynceus maclayeanus* and *Eulimnadia dahli*) are ecologically separated by differences in seasonal occurrence, habitat and feeding requirements. The high diversity in south-western Australia is explained by its great age, rock pools acting as refugia in dry climatic periods, and separation from eastern Australia.

**Key words**: *Branchinella longirostris, Limnadia badia, Caenestheriella maraie, Lynceus maclayeanus,* niche separation, co-occurrences, south-western Australia.

## Introduction

Rock holes, or gnammas as they are known throughout Western Australia and beyond (Bayly 1999), are common and widespread landscape features in Australia. This is particularly so on granitic rocks and in arid/semiarid regions (Carnegie 1898; Bayly 2002).They are semantically equivalent to 'weather pits,' 'solution pits,' 'granite pits,' 'rock basins,' 'pot holes,' 'pits,' and 'pans' (in context, not clay pans or playas) (Smith 1941; Twidale & Campbell 1993; Brendonck *et al.* 2000, Graham in press).

The few studies on Australian gnammas have focused on their geomorphology (Twidale & Corbin 1963; Campbell & Twidale 1995) and community ecology (Bayly 1982, 1997; Bishop 1974; Pinder *et al.* 2000), though Bishop (1967a, 1967b, 1969) considered the autoecology of the conchostracan *Limnadia stanyleyana*. Early taxonomical studies by Wolf (1911) described the anostracan *Branchinella longirostris* and the conchostracan *Limnadia badia* from granitic gnammas in south-western Australia, and more recently Webb & Bell (1979) described *Limnadia urukhai* from similar pools in south-eastern Queensland. Otherwise references to large branchiopods of Australian gnammas are little more than species lists, sometimes incompletely identified (Main 1967; Jones 1971; Pinder *et al.* 2000; Bayly 2001, Timms 2002; Timms & Geddes 2003).

The above studies point to a much richer fauna in south-western Western Australia than elsewhere in Australia. Therefore the aim of this paper is to systematically investigate the composition and biogeography of the large branchiopod fauna of gnammas in southwestern Australia, but in a context of Australia as a whole.



## Methods

Fifty-two granitic outcrops throughout south-western Western Australia, bounded by Cue in the north, near Balladonia in the east, Holland Rocks in the south and near Perth in the west (Fig. 1) were visited between July and September 2003. The northern, eastern and western limits are near the edge of major outcrops of granitic rocks (Myers 1997); in the south there are many more significant outcrops south of Wagin-Pingrup, but previous studies (Bayly 1982, 1997; Pinder *et al.* 2000) have not recorded large branchiopods on them.

My previous field experience and that of Bayly (1997) suggested larger gnammas had more invertebrate species, and that pools > 10–20 cm deep when full and one to two metres diameter were large enough to contain most species. Stochastic events and different seasonal development strategies may limit the fauna actually present at anyone time. For maximum diversity, pools were visited when full or nearly so and only those deeper than 10 cm and larger than 50 cm diameter were targeted, with an emphasis, if possible, on larger pools. To simplify fieldwork and analysis, gnammas were divided into four types:

- Small shallow pan gnammas generally 0.5 to 1 m in diameter, and 10–20 cm deep when full.
- Larger, deeper pan gnammas generally 2–5 m in diameter and 20–40 cm deep when full.
- Pit gnammas which although of small diameter (50 cm to 1–2 m), were deeper than 0.25 m, often up to 1–2m deep.
- A variety of other contact pools adjacent to the base of the rock or artificially dammed on the rock. Most had significant contact with soil and were > 2 m diameter.

At each granitic outcrop up to 10 smaller pans and up

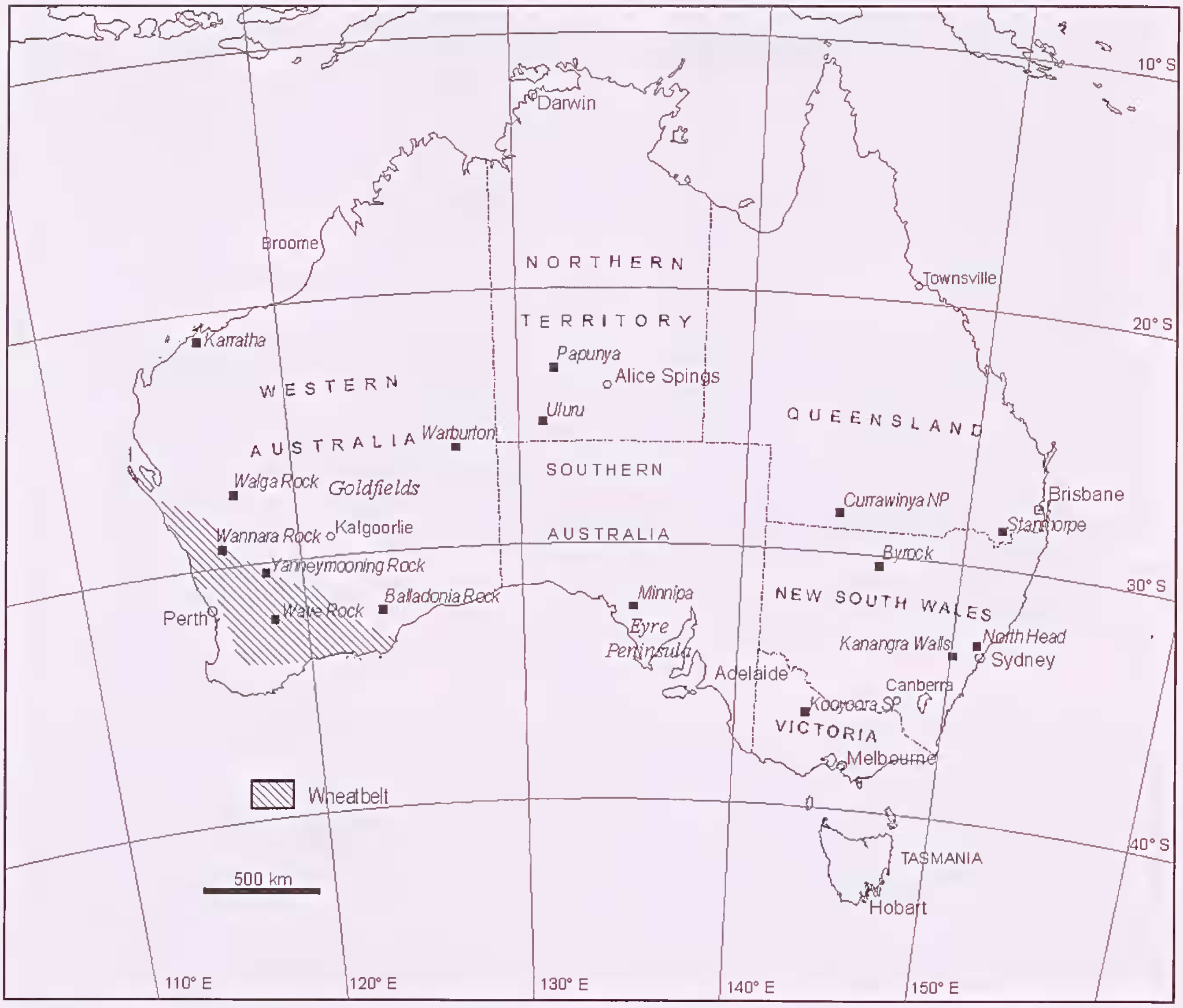


**Figure 1.** Map of localities sampled for large branchiopods in south-western Australia.

to 10 larger pans, if available, were sampled together with any pit gnammas and associated pools that were found on the rock (some pit gnammas are hidden by capping stones and difficult to locate). A round household sieve, 17 cm in diameter, 7 cm deep and of mesh size 1.4 mm, was moved to and fro through each pool for 1–3 minutes depending on numbers caught and any large branchiopods caught transferred to a sorting tray, and then preserved in 80 % ethanol.Species were recorded on a presence-absence basis for each pool.

I adopted a similar approach for some granitic outcrops (Mt Wudinna, Turtle Rock, Polda Rock, Pooncarra Rock, Pildappa Rock and Peella Rocks) near Wudinna and Minnipa in the Upper Eyre Peninsula, South Australia. Only a summary of this work is presented here. In the winter of 2004, I revisited some of the Western Australian sites studied in 2003 plus many others. This time only a general assessment was made of species present on each granite outcrop and the data used to fill out the species distribution maps.

Some material from other rock pools, or collected at other times of the year from gnammas in Western Australia were made available to this study by colleagues (see Appendix 1). Other data were gleaned from the literature and from collections in the Western Australian Museum (WAM).

## Results

Four species (*Branchinella longirostris, Limnadia badia, Caenestheriella mariae* and *Lynceus macleayanus*) were collected commonly from most of the 52 granite outcrops studied in Western Australia (Table 1). The first three are obligate inhabitants of gnammas and probably do not occur much beyond the distributions shown in Figures 2–4. The core area for these three species is an irregular oval area bounded by Kalgoorlie, Balladonia, Ravensthorpe, Wagin, Northam, Dallwallinu and Mt Magnet, with minor deviations for each species. *Caenestheriella mariae* is the most limited with no populations found in the southwest, *B. longirostris* also is apparently absent from the southwest and the far

**Table 1**

Distribution and numbers of large branchiopods in granitic rock pools in Western Australia as determined by field work in 2003.

| Rock No. | Outcrops Name | Deep pans No. | Bl | Lb | Cm | Lm | Tr | Shallow pans No. | Bl | Lm | Cm | Pits No. | Lm | Other pools No. | Bl | Lm | Cm | Cp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Newmans Rks | 2 | 1 | | 1 | | | 10 | | 1 | | | | | | | | |
| 2 | Disappointment Rks | 10 | 3 | 7 | | | | 10 | | 4 | | | | | | | | |
| 3 | McDermid Rks | 10 | 7 | 8 | 1 | | | 10 | | 6 | | | | | | | | |
| 4 | Bushfire Rks | 2 | 1 | 2 | 1 | | | 10 | | 4 | | | | | | | | |
| 5 | King Rks | 5 | | 5 | 2 | | | 10 | | 6 | | | | | | | | |
| 6 | Graham Rks | 4 | | | | | | 5 | | | | | | | | | | |
| 7 | Wave Rk | 10 | 2 | 6 | | | | 10 | | 1 | | | | | | | | |
| 8 | Anderson Rks | 10 | 5 | 7 | | | | 10 | | 4 | | 3 | | | | | | |
| 9 | Frog Rk | 10 | 2 | 4 | | | | 10 | | 1 | | | | | | | | |
| 10 | Jilbadgie Rk | 10 | 4 | 6 | | | | 10 | | 3 | | | | | | | | |
| 11 | Strawberry Rks | 1 | 1 | 1 | | | | 5 | | 4 | | | | | | | | |
| 12 | Moorine Rk | 2 | 2 | 2 | | | | 5 | | 3 | | | | | | | | |
| 13 | Coarin Rk | 2 | | 2 | | | | 5 | | 2 | | | | | | | | |
| 14 | Bulgin Rk | | | | | | | 2 | | | | | | | | | | |
| 15 | Yorkrakine Rk | 5 | 3 | 4 | | | | 10 | | 4 | | | | | | | | |
| 16 | Yarragin Rks | 5 | 3 | 3 | | | | 10 | | 3 | | | | | | | | |
| 17 | Elachbutting Rks | 10 | 3 | 6 | 2 | | | 10 | | 2 | | | | | | | | |
| 18 | Baladjie Rks | 1 | 1 | 1 | 1 | | | 10 | 1 | 3 | | | | | | | | |
| 19 | Weowannie Rks | 5 | 4 | 4 | | | | 5 | | 1 | | | | | | | | |
| 20 | Sanford Rks | 10 | 3 | 4 | | | | 5 | | 2 | | | | | | | | |
| 21 | Corrigin Rk | | | | | | | 10 | | 1 | | | | | | | | |
| 22 | Boyagen Rk | 2 | | | | | | 5 | | | | | | | | | | |
| 23 | Sullivan Rk | | | | | | | 2 | | 2 | | | | | | | | |
| 24 | Petrudor Rk | | | | | | | 10 | | 4 | | | | 2* | | 2 | | 1 |
| 25 | Cleary Rk | | | | | | | 10 | | 5 | | | | 1^ | | 1 | | |
| 26 | Scotsmans Road' | | | | | | | 10 | | 5 | | 2 | 1 | | | | | |
| 27 | Washington Rks | | | | | | | 10 | | 4 | | 2 | 1 | | | | | |
| 28 | Remlap old hstead' | 6 | 2 | 2 | 1 | | | 10 | | 2 | | | | | | | | |
| 29 | Paynes Find Rks | 10 | 7 | 4 | 2 | | | 10 | | 3 | | | | 1* | | 1 | | |
| 30 | Wanarra Rks | 10 | 3 | 1 | 2 | | | 10 | | | 1 | | | 1^ | 1 | 1 | 1 | |
| 31 | Green Rk | 0 | | | | | | 10 | | | | | | 1* | | 1 | | |
| 32 | Wardagga Rk | 10 | 6 | 2 | 4 | | | 10 | | 1 | 1 | | | 5* | | 1 | | |
| 33 | Daggar Hills | 10 | 3 | 1 | | | | 10 | | | | | | | | | | |
| 34 | Walga Rk | 4 | 2 | | 4 | | 1 | 10 | | | | | | | | | | |
| 35 | Afghan Rk | 0 | | | | | | 8 | | | | | | | | | | |
| 36 | Barlongi Rk | 0 | | | | | | 0 | | | | | | | | | | |
| 37 | Trainer Rks | | | | | | | 10 | | | | | | 1 | | | | |
| 38 | Rainy Rks | | | | | | | 10 | | | | | | 2 | | | | |
| 39 | Old Rainy Rks | 5 | 1 | 3 | | | | 10 | | | | 1 | 1 | | | | | |
| 40 | Hospital Rks | 10 | 4 | 2 | | | | 10 | | 1 | | | | | | | | |
| 41 | 25 Mile Rks | | | | | | | 10 | | 4 | | | | | | | | |
| 42 | Buldania Rk | 3 | | 1 | | | | 10 | | 2 | | 5 | 3 | | | | | |
| 43 | McPherson Rk | 10 | 2 | 6 | | 1 | | 10 | | 1 | | | | | | | | |
| 44 | Lilian Stokes Rks | 10 | 1 | 4 | 1 | 1 | | 10 | | 2 | | | | | | | | |
| 45 | Mt Madden | 10 | 1 | 3 | | 1 | | 10 | | | | | | | | | | |
| 46 | Dingo Rk | | | | | | | 10 | | 7 | | | | | | | | |
| 47 | Jilakin Rk | | | | | | | 10 | | 1 | | | | | | | | |
| 48 | Puntapin Rk | | | | | | | 10 | | 2 | | | | | | | | |
| 49 | Yillaminning Rk | 0 | | | | | | 0 | | | | | | | | | | |
| 50 | Boulder Rk | 0 | | | | | | 2 | | | | | | | | | | |
| 51 | Holland Rks | 10 | | 9 | 1 | 1 | | 10 | | 3 | | 2 | 2 | | | | | |
| 52 | Xantippe Rks | 6 | 5 | 6 | | | | 10# | | | | | | | | | | |

*plunge pools
^artificial dam
#all dry when visited

No = number of pools sampled; Bl = *Branchinella longirostris*, Lb = *Limnadia badia*, Cm = *Caenestheriella mariae*(recorded as *Cyzicus* sp. by Bayly (1997) and Pinder (2000)); Cp = *Caenestheriella packardi*; Lm = *Lynceus macleayanus*, Tr = *Triops* near *australiensis*

southeast, while *Limnadia badia* penetrates further south and southeast than other species (Figures 2–4). *Lynceus macleayanus* occurs within this area (Fig. 5), and elsewhere in the state and in South Australia, but almost always in gnammas or pools adjacent to rock outcrops (M. Zofkova, pers. comm.). A fifth species, *Triops* sp. near *australiensis* occurred rarely in one pool on Walga Rock in 2003 and 2004 (it was also there in 2001, author's unpubl.data), and also in many pools on Ballan Rock in 2004.In addition this species is known from a pan in the Pilbara (northwestern WA)(A. Pinder, pers.comm.).

Detailed analysis of occurrence data on each granite outcrop showed each of the common species had different habitat preferences (Table 1). *Branchinella*

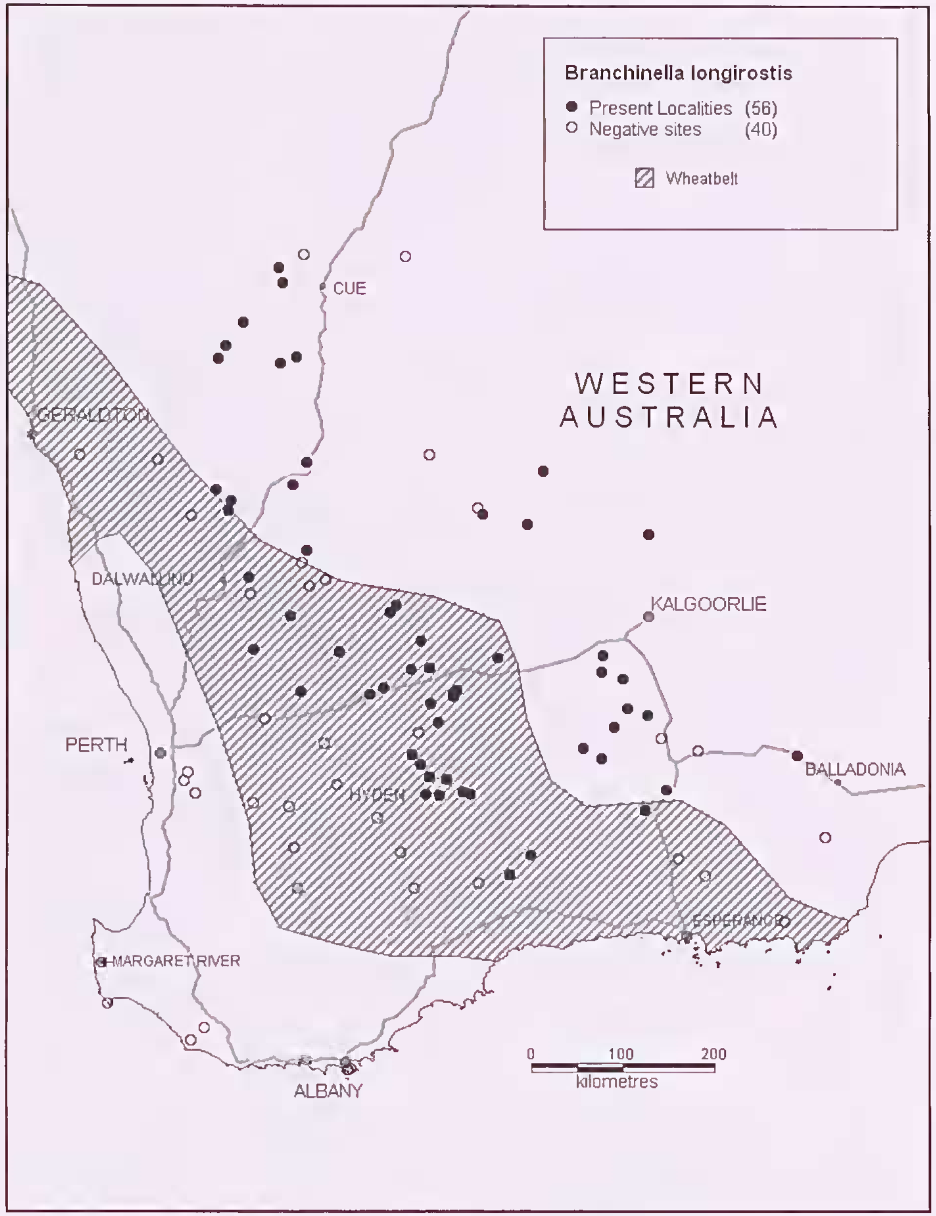


Figure 2. Distribution of *Branchinella longirostris* in south-western Australia.

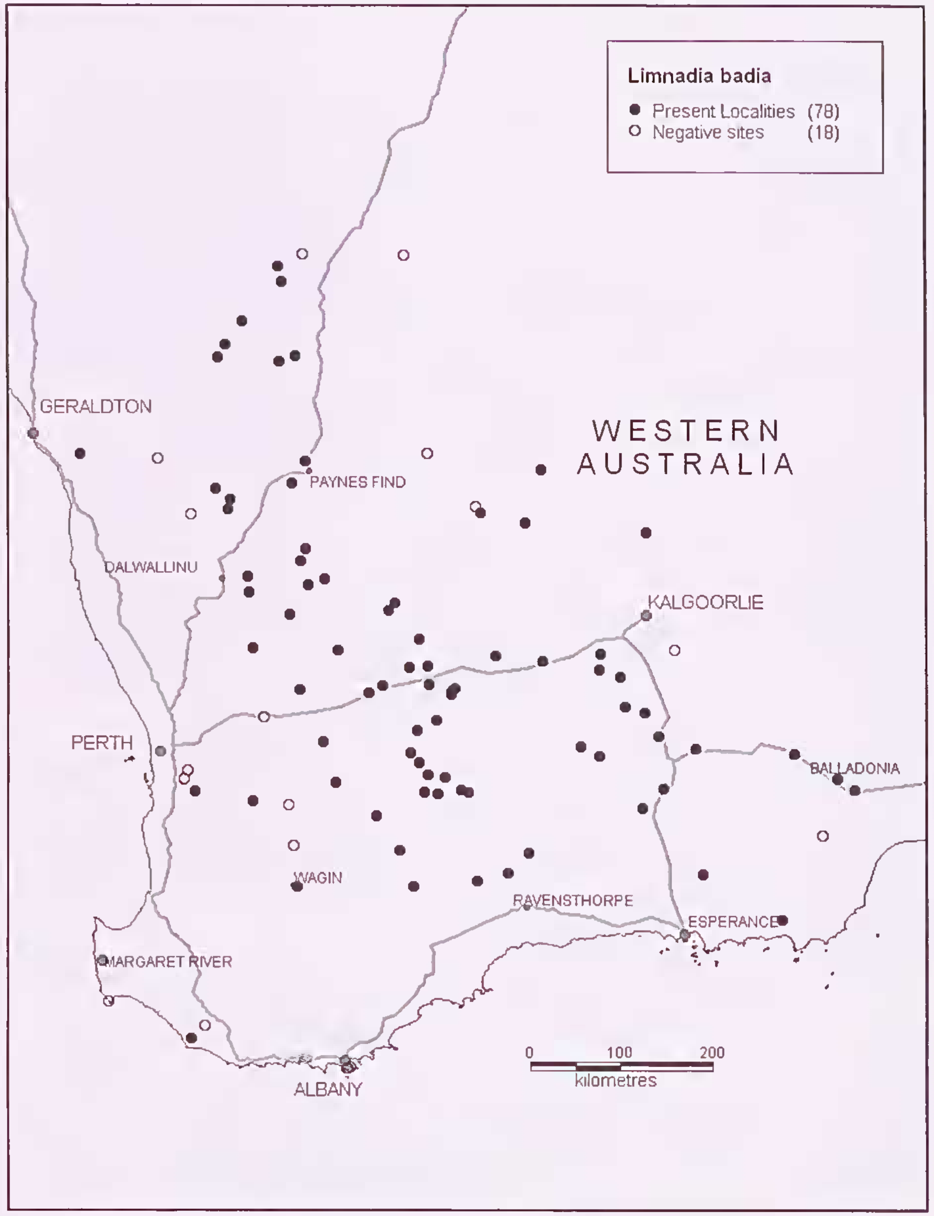


Figure 3. Distribution of *Limnadia badia* in south-western Australia.

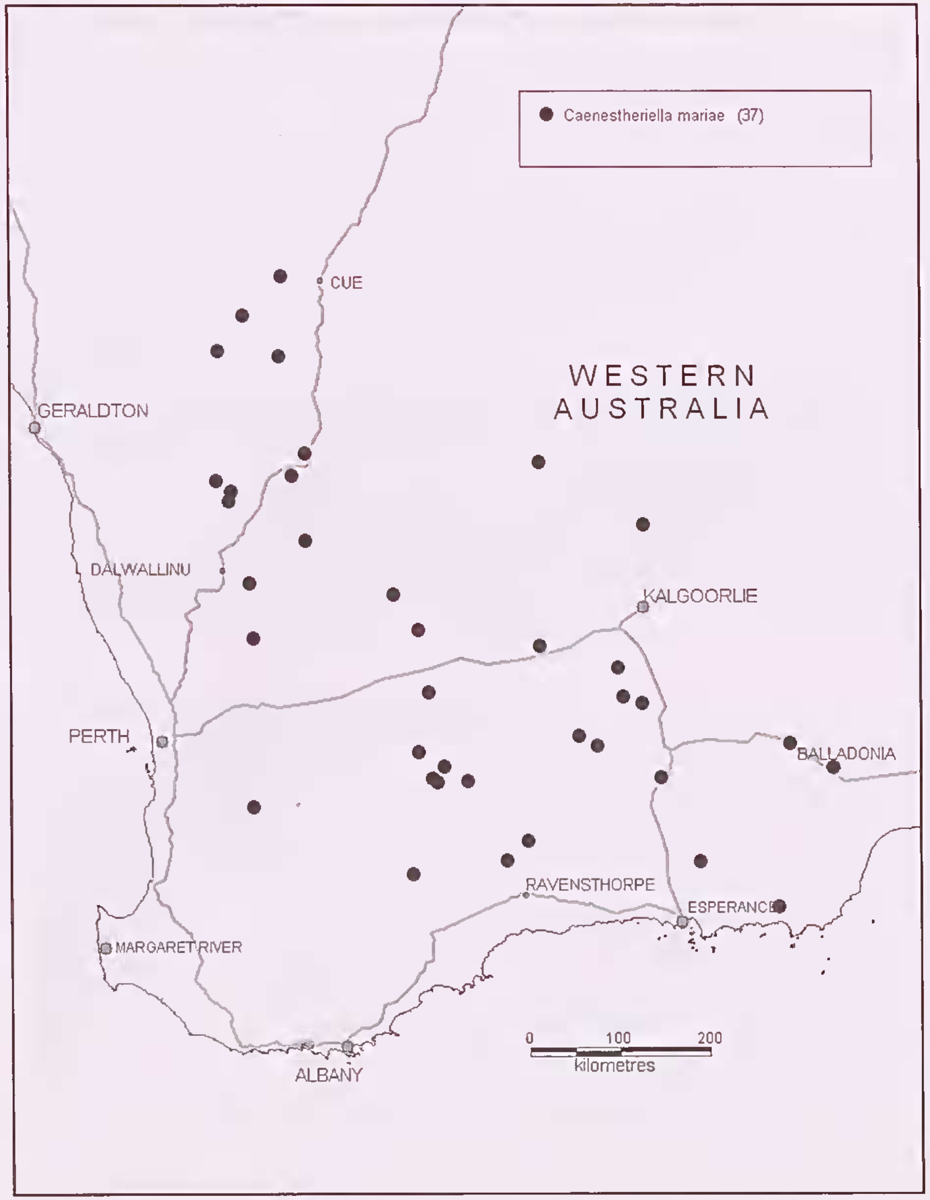


Figure 4. Distribution of *Caenestheriella mariae* in gnammas in south-western Australia.

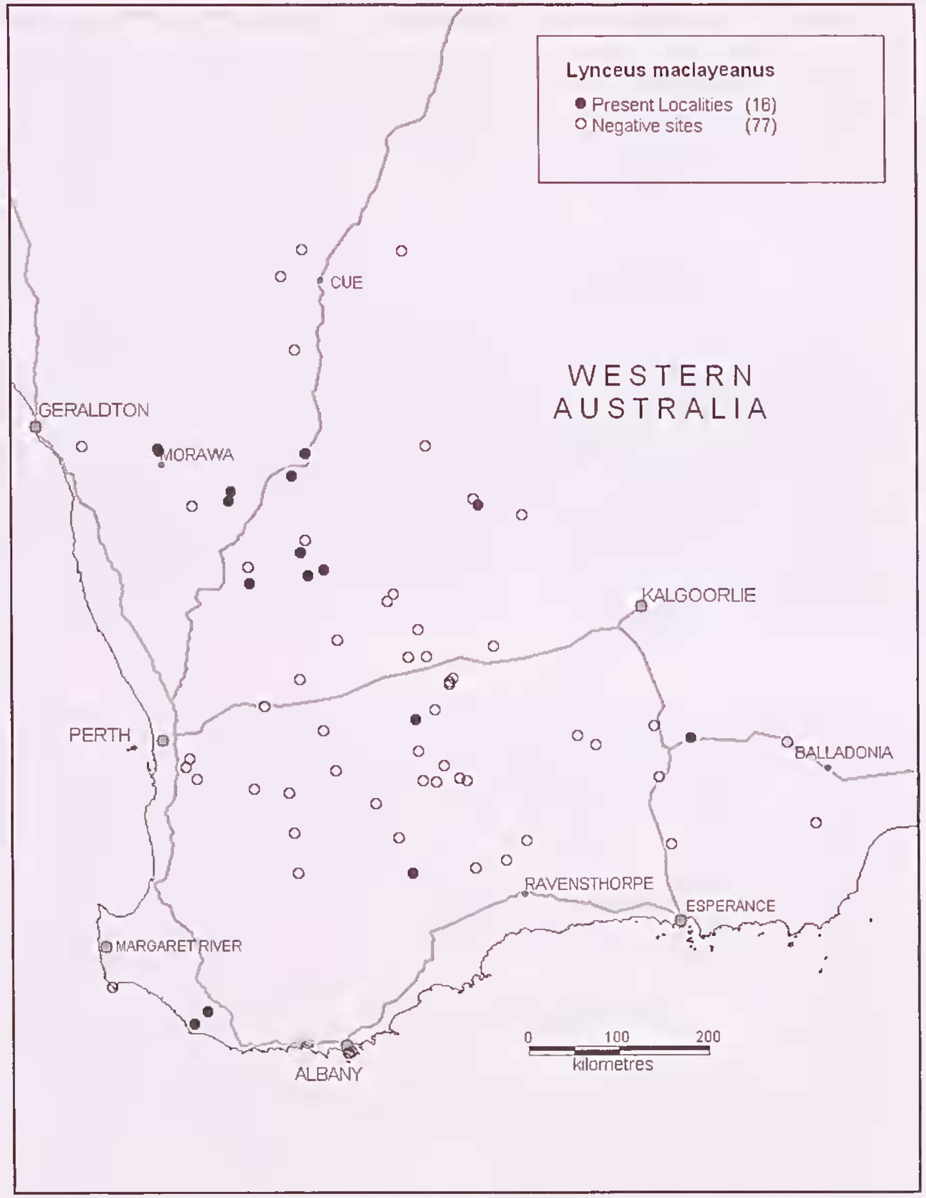


Figure 5. Distribution of *Lynceus macleayanus* in gnammas in south-western Australia.

*longirostris* lived almost exclusively in deeper pans (41% of deeper pans on rocks contained the species – range 20–100% of pools on any one rock), and hardly ever was found in shallower pans (< 1% of shallower pans on rocks with the species), never in deep pit gnammas, and only once in a large contact pool. *Caenestheriella mariae* had similar narrow habitat requirements to *Branchinella longirostris* but was not as common – 10% occurrence in deeper pans, and << 1% of shallower pans. It did not occur in deep pits and only once in a contact pool. *Limnadia badia* also was not found in deep pits and larger contact pools, but was much more common overall and more tolerant of shallower conditions [57.0% of deeper pans (range 10–100% on individual rocks), and 31.8% of shallower pools (range 10–100% on individual rocks)]. In contrast to these three species, *Lynceus macleayanus* is a deeper water specialist, being almost confined to deeper pits and larger contact pools (55.5 % of pits and 54.5% of contact pools and not in shallower pans and found in only one deeper pan).

Of the 330 occurrences of large branchiopods in 679 pools in the study area, there were 63 pools with multiple species. The most common co-occurrence (42 sites) was between *B. longirostris* and *L. badia*, and the next (7 sites) between *L. badia* and *Caenestheriella mariae*. There were seven sites with three species co-occurring. The mean number of species per pool was 0.5.Field observations suggest that the three most common species, and the ones most likely to co-occur, feed differently – *B. longirostris* filter feeds in the water column, *L. badia* feeds mainly on bottom debris and *Caenestheriella mariae* feed largely by scraping algae from hard rock surfaces.

The study of a few granite outcrops on Eyre Peninsula, South Australia, yielded only three populations of *Lynceus macleayanus* in deep gnamma pits (two on Pildappa Rock and one on Pooncarra Rock).Pans on these and the other rocks were rarely deeper than 20 cm and larger than 2 m diameter, and did not yield any large branchiopods in winter.

The above data were based on the 2003 study. The 2004 visit to many of the Western Australian sites reaffirmed occurrences, but provided a slightly different impression of relative abundance and distribution of the different species. There were more records of *Caenestheriella mariae* than in 2003 and *Triops* near *australiensis* was common on Walga and Ballan Rocks.*Branchinella longirostris* was often found in shallower pools than in 2003, explained by the pools drying because of evaporation. *B. affinis,* and occasionally *B. wellardi,* occurred in pools at the base of rocks, and at Dunn Rock, south of Newdegate, *B. affinis* occured in gnammas well away from the base, but elevated only a few metres.Contrawise, *B. longirostris* occurred only in gnammas.

Summer collections from gnammas in both Western Australia and Upper Eyre Peninsula in South Australia, have occasionally yielded *Eulimnadia dahli*. After summer storms in March 2003, some pan gnammas in the northern Wheatbelt (Appendix 1) had this species, but no other large branchiopods (M.Zofkova, pers. comm.). Pans on Corrobinnie, Peella and Pildappa Rocks on Eyre Peninsula also had populations of *E. dahli* after a storm filled pans in November 2003 (author, unpubl. data). Indicative lengths of *Eulimnadia dahli* are ca.4–6 mm. One population of *Lynceus macleayanus* also continued to exist in November, 2003 in a large pit gnamma on Pildappa Rock, which apparently had water continuously since winter. All Eyre Peninsula pools were dry in February 2004. Following a storm in mid April, 2004, *Eulimnadia dahli* (and *B. longirostris*) were found in gnammas on King Rock (J. Hill, pers.comm.). *Eulimnadia dahli* has also been collected from Karratha Rock Hole in the Pilbara (A. Pinder, pers.comm.), and from Mt Samuel (WAM), in the far northwest and remote inland respectively, of Western Australia (Fig. 1; Appendix 1).

Other WAM records of gnamma species pertain mainly to *Lynceus* n.sp. at various sites in the central deserts of WA (including at Mt Samuel) and *Lynceus* sp. in gnammas in the limestone of the Nullabor Plain. The Mt Samuel site also harboured the anostracan *Streptocephalus* sp.

Searching by the author during 2000–2004 in selected gnammas in eastern Australia (Fig. 1) uncovered no species in granitic pans at Kooyoora State Park, via Bendigo, Victoria; *Limnadia stanleyana* in pools on sandstone at Kanangra Walls in the Blue Mountains, NSW; *Streptocephalus* sp. from a pool adjacent to granite at Byrock, NSW; *Lynceus* sp. from a rock pool in metamorphic rock at Hood Range, Currawinya National Park, southwestern Queensland; *Caenestheriella packardi* from a deep gnamma (= rockwell) on Rockwell Station, southwestern Queensland, and *Limnadia urukhai* in granitic pans near Stanthorpe, Queensland.*Limnadia stanleyana* also has been found in sandstone pools in the Budawang Mountains west of Ulladulla, NSW (M. Fielder, pers. comm.).

## Discussion

Across Australia, sixteen species of large branchiopods have been recorded from gnammas (Table 2). Eleven are judged to be of low or very low frequency of occurrence, but given the right conditions some can become common at one or a few sites, *e.g., Branchinella latzi* on Uluru, NT, *Branchinella basispina* on pools adjacent to granite outcrops on the western edge of the Nullabor,WA, *Lynceus* n. sp. in deep non-granitic gnammas of the central deserts in WA, *Limnadia stanleyana* in pools sandstone mountains west and south of Sydney, NSW and *Branchinella urukhai* in the Stanthorpe area of Queensland. Others occur at more sites and are seen more often so are judged as being 'moderately frequent' in occurrence *e.g., Eulimnadia dahli* in Western Australia and South Australia, *Caenestheriella mariae* in Western Australia, *Lynceus macleayanus* mainly in granitic gnammas throughout the western inland. Two are judged as being of 'high' frequency as they are often encountered in the right season over a large area, *e.g.,* both *Branchinella longirostris* and *Limnadia badia* in the Wheatbelt and Goldfields of Western Australia.

Many of these species are obligate gnamma inhabitants. These include *Limnadia urukhai* in Queensland/New South Wales, *Branchinella longirostris, Limandia badia,* and *Caenestheriella mariae* in Western Australia. It is possible that *Branchinella basispina, Limnadia stanleyana,* the new species of *Lynceus* in deep

**Table 2**

Large branchiopods in gnammas in Australia.

| Species | Distribution in rock pools | Frequency of occurrence | Source |
|---|---|---|---|
| *Branchinella affinis* | Southern WA and southern NT | Very low | Pinder *et al.* 2000; Timms & Geddes 2003 |
| *Branchinella basispina* | western edge of Nullabor Plain, WA | Low, localized | Timms & Geddes 2003 |
| *Branchinella latzi* | Southern NT | Low, localized | Timms & Geddes 2003 |
| *Branchinella longirostris* | Wheatbelt and Goldfields of WA | High | This study; Timms 2003 |
| *Branchinella lyrifera* | NE edge of WA Wheatbelt | Very low | Pinder *et al.* 2000 |
| *Streptocephalus spp.* | Cent. Australia, west. Murray-Darling Basin | Low, widespread | Bayly, 2001; Author, unpublished |
| *Lynceus macleayanus* | WA, SA, west Qld | Moderate | M. Zofkova, unpubl. data; This study; Bayly 1991 |
| *Lynceus* n.sp. | Central deserts of WA | Low, localized | M. Zofkova Unpubl.data |
| *Eulimnadia dahli* | WA, Eyre Peninsula, SA | Moderate | This study |
| *Limnadia badia* | Wheatbelt and Goldfields of WA | High | This study. |
| *Limnadia stanleyana* | Sydney Basin | Low, localized | Bishop 1974 |
| *Limnadia urukhai* | Granite belt of southern Qld and adjacent NSW. | Low, localized | Webb & Bell, 1979 |
| *Caenestheriella mariae* | Wheatbelt & Goldfileds of WA | Moderate | This study |
| *Caenestheriella packardi* | A pit gnamma Rockwell Station; southwest Qld. | Very low, localized | Author, unpublished data |
| *Lepiduris apus viridus* | Southwest WA | Very low | Jones 1971 |
| *Triops* sp near *australiensis* | Northwestern WA | Very low | This study |

non-granitic gnammas of the remote inland, and the species of *Triops* in pools on Walga Rock, Ballan Rock and Karratha Rock may also qualify, but more data are needed for a confident classification. *Lynceus macleayanus* is also a gnamma specialist but not an obligate inhabitant as there are many old records in other habitats (Richter & Timms, 2005). It lives almost exclusively in deeper pools as shown in Table 1 and noted in Bayly (1997). Many species, while commonly utilizing gnamma habitat, are abundant in other habitats, including *Eulimnadia dahli, Branchinella latzi* and *B. affinis. Branchinella lyrifera* and *Lepidurus apus viridis* appear to be accidental occurrences as there is only one occurrence of each and both are common in a wide range of habitat types. Not enough is known on *Streptocephalus* spp. to know their habitat specificity. Finally, as shown by Timms and Geddes (2003), there seems to be a recent change in the dominant species on Uluru, from *Branchinella latzi* to *B. affinis.*

Western Australia has by far the most species of large branchiopods in gnammas (12) compared with the Northern Territory (3), New South Wales (3), Queensland (3), South Australia (2), Victoria and Tasmania (0). As for other aquatic invertebrates that are more speciose in southwestern WA than elsewhere *e.g., Parartemia* (Remigio *et al.* 2001), *Branchinella* (Timms 2002), cladocerans (Frey 1991; Hebert & Wilson 2000), ostracods (Halse & McRae 2004), the explanation for the west of Western Australia lies in the great age of a stable landscape. There has been no catastrophic impacts of marine inundation, little volcanism affecting the bulk of the Yilgarn Craton, or glaciation since the Permain Other contributing factors include adaptation to refugia in times of climatic stress (in this case the more reliable gnammas) and genetic isolation from eastern Australia (Pinder *et al.* 2004).

In concert with the less diverse branchiopod fauna in Australia than in similar places worldwide (Bănărescu 1995; Williams 1981), few species occur in most Australian ganammas except those in Western Australia. By contrast southern Africa has at least six species of *Branchiopodopsis* living in rock pools (Hamer & Appleton 1996) and *Leptestheriella ineremis* (L. Brendonck, pers. com.), while in western USA and adjacent Mexico *Branchinecta lindahli, B. packardi. B. lynchi, B. coloradensis, Eubranchipus oregonus, Streptocephalus texanus, S. dorothae, Thamnocephalus platyurus, Eulimnadia texana, Leptestheria compleximanus* and *Triops longicaudatus* occur in rock pools (Baron *et al.* 1998; Belk 1991; Eng *et al.* 1990; Eriksen & Belk 1999; Graham in press; C. Rogers pers. comm.). At least some of these are gnamma specialists, including *Branchiopododsis wolfi* in southern Africa (Brendonck *et al.* 2000) but none in USA (C. Rogers pers. comm.). It is feasible that south-western Australia may have more species restricted to gnammas than elsewhere, which again probably is a reflection of the geological stability, climate variability and continuous existence of inselbergs and their gnammas over long periods of geologic time (Twidale & Campbell 1993). I emphasise geological stability because in fact the climate has been quite variable and it is probably a combination of a stable geology but instable climate that has led to high diversity – *i.e.* each climatic phase may have led to diversification but there hasn't been events like glaciation, volcanism and marine inundation (other than around the coast) to reset the fauna.

At the recent International Large Branchipod Symposium, held in Toodyay, Western Australia, in 2004 (where this paper was originally presented), a participant criticised my comment about the great age of the Yilgarn being a cause of high diversity because 'it is instability that causes speciation not stability' but I think in the case of ancient geological stability it could help preserve diversity caused by repeated climatic variation by protecting the resulting diversity from extinction-causing catastrophic events.

It is noteworthy that among large branchiopods throughout the world, anostracans tend to dominate rock pools and notostracans are particularly scarce, despite the later's adaptations for living in such temporary environments. The contention by Main (1997, 2000) that *Triops* is a characteristic inhabitant of rock pools in Western Australia is not supported by the present data or work by Bayly (1982, 1997) and Pinder *et al.* (2000). Nevertheless, there are persistent populations of *Triops* on three rocks in the north of the state, and B. Knott (pers. comm.) contends the presence of notostracans on granite out crops in southwest Western Australia twenty years ago.

Spinicaudtan clam shrimps seem to be particularly common and diverse in Australian rock pools compared with those in southern Africa and western USA (Hamer & Appleton 1996; Baron *et al.* 1998; Brendonck *et al.* 2000; Graham in press), though this seems to contradict the statement above about relatively low diversity of large branchiopods in Australian rock pools. Six species, as well as two laevicaudatan clam shrimps are known, with differentiation across Australia. By contrast there is only one specialist anostracan (*B. longirostris*) which is restricted to an apparent centre of speciation in southwestern Australia (Timms 2002), though a few other anostracans occasionally live in gnammas.This species never occurs in nearby mud pools, and if these contain an anostracan it is likely to be the closely related *B. affinis*.

Resources in gnammas are limited and there is intense competition for them, *e.g.*, Brendonck *et al.* (2002). Co-occurrences of branchiopods seem to be less common in gnammas compared with those in other waters.Studies on North American and African gnammas rarely report co-occurrences and do not quantify them (Baron *et al.* 1998; Brendonck & Riddoch 1997; Brendonck *et al.* 2000; Eng *et al.* 1990; Eriksen & Belk 1999; Hamer & Appleton 1996). In eastern Australia no co-occurrences have been noted, but in south-western Australia 24% of pools with at least one large branchiopod had additional species. Comparative figures for all types of freshwater waterbodies with at least one large branchiopod in the wheatbelt and Carnarvon basin are 24% and 76% respectively (A. Pinder, pers.comm.). For anostracans alone there are no recorded co-occurrences in gnammas, compared with 4.9% in all wetlands of theWA Wheatbelt, 31.8% in all wetlands of the Carnarvon basin (A. Pinder, pers.comm.) and 51% of all wetlands in the Paroo in eastern Australia (Timms & Sanders 2002). For clam shrimps, there are 3.8% of gnamma sites with co-occurrences, compared with 48% among other wheatbelt sites, 11.1% of other Carnarvon sites (A. Pinder, pers.comm.) and 20.4 % of other sites in the Paroo (Timms & Richter 2002).

When there are co-occurrences in south-western Australia, the participants feed differently. Moreover there is some seasonal separation of species, with *Eulimnadia dahli* a summer species and the remainder winter-spring species. Interestingly a parallel situation is known among Chironomidae in these gnammas – *Paraborniella* sp occurs in summer and *Allotrissocladius* spp. are active in winter (Bayly 1999).

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## Appendix

Sites where species of large branchiopods have been found in Western Australia

| Name | nearest town/ locality | latitude | longitude | *Branchinella longirostris** | *Limnadia badia** | *Caenestheriella mariae** | *Lynceus macleayanus** | Other Species |
|---|---|---|---|---|---|---|---|---|
| Karratha Rock | Karratha | 20 55 | 116 42 | | | | | *Eulimnadia dahli* and *Triops* near *australiensis*-A. Pinder. |
| Mt Samuel | Warburton | 25° 54' | 125 58 | | | | | *Lynceus* n. sp., *E. dahli*, *Streptocephalus sp.*- WAM |
| 170 km SE Warburton | Warburton | 27 00 | 125 05 | | | | | *Lynceus* n.sp.- WAM |
| Ryans Bluff | Warburton | 27 14 | 126 25 | | | | | *Lynceus* n.sp.- WAM |
| Walloo Hill | Cue | 27 15 | 117 26 | 2004 | 2004 | | | |
| Walga Rock | Cue | 27 24 | 117 28 | 2003/4 | 2004 | 2003/4 | | *Triops* near *australiensis* |
| Dalgaranga Rocks | Cue | 27 46 | 117 01 | 2004 | 2004 | 2004 | | |
| Chinaman Rock | Yalgoo | 28 00 | 116 49 | 2004 | 2004 | | | |
| Goolthan Hill | Yalgoo | 28 07 | 116 44 | 2004 | 2004 | 2004 | | |
| Daggar Hill | Mt Magnet | 28 08 | 117 36 | 2003 | 2003 | | | |
| Ballan Rock | Mt Magnet | 28 11 | 117 25 | 2004 | 2004 | 2004 | | *Triops* near *australiensis* |
| Bilya Rock | Mingenew | 29 00 | 115 08 | | M.Zofkova | | | |
| Mt East | Laverton | 29 03 | 122 40 | | | | | *Lynceus* n.sp.- WAM |
| Paynes Find Rocks | Paynes Find | 29 10 | 117 40 | 2003/4 | 2003/4 | 2003 | 2003 | |
| Yendang Rocks | Menzies | 29 19 | 120 19 | 2004 | 2004 | 2004 | 2004 | |
| Wardagga Rock | Paynes Find | 29 23 | 117 30 | 2003 | 2003 | 2003 | | |
| Camel Soak | Perenjori | 29 24 | 116 38 | 2004 | 2004 | 2004 | | |
| Wanarra Rock | Perenjori | 29 31 | 116 48 | 2003/4 | 2003/4 | 2003/4 | 2003 | *Eulimnadia dahli* - M.Zofkova |
| Green Rock | Perenjori | 29 37 | 116 46 | 2004 | 2003/4 | 2004 | 2003 | *Eulimnadia dahli* - M.Zofkova |
| Old Rainy Rocks | Menzies | 29 44 | 119 37 | 2003 | 2003 | | 2003 | |
| Hospital Rocks | Menzies | 29 50 | 120 07 | 2003 | 2003 | | | |
| 25 Mile Rocks | Menzies | 29 57 | 121 29 | 2004 | 2004 | 2004 | | |
| Old Remlap Rocks | Beacon | 30 02 | 117 38 | 2003/4 | 2003/4 | 2003/4 | | |
| Washington Rocks | Beacon | 30 09 | 117 34 | | 2003/4 | | 2003 | |
| Xantippe Rocks | Dallwallinu | 30 17 | 116 58 | 2003/4 | 2003/4 | | | |
| Yellari Rocks | Beacon | 30 20 | 117 50 | | 2003/4 | | 2003 | |
| Cleary Rocks | Beacon | 30 23 | 117 39 | | 2003/4 | | 2003 | |
| Petrudor Rock | Dallwallinu | 30 26 | 116 58 | | 2003/4 | 2003 | 2003 | |
| Elachbutting Rock | Beacon | 30 36 | 118 37 | 2003/4 | 2003/4 | 2003 | | *Eulimnadia dahli* - M.Zofkova |
| Yanneymooning Rocks | Beacon | 30 40 | 118 33 | A. Pinder | A. Pinder | | | *Eulimnadia dahli* - M.Zofkova |
| Newcarlbeon Rock | Kalannie | 30 40 | 117 25 | 2004 | 2004 | | | |
| Baladjie Rock | Bullfinch | 30 57 | 118 53 | 2003/4 | 2003/4 | 2003/4 | | |
| Uberin Rock | Dowerin | 30 59 | 116 59 | 2004 | 2004 | 2004 | | |
| Yarragin Rock | Trayning | 31 02 | 117 57 | 2003 | 2003 | | | |
| Weowannie Rocks | Yellowdine | 31 08 | 119 45 | 2003/4 | 2003/4 | 2004 | | |
| Gnarbine Rocks | Coolgardie | 31 08 | 120 57 | 2003 | 2003 | | | |
| Boorabbin Rocks | Yellowdine | 31 12 | 120 17 | | 2003 | | | |
| Moorine Rock | Westonia | 31 13 | 118 59 | 2003/4 | 2003/4 | | | |
| Sandford Rock | Westonia | 31 14 | 118 46 | 2003 | 2003 | | | |
| Quainine Rocks | Coolgardie | 31 16 | 121 04 | M. Zofkova | | | | |
| Victoria Rock | Coolgardie | 31 17 | 120 56 | 2003 | 2003 | | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Burra Rock | Coolgardie | 31 22 | 121 11 | 2004 | 2004 | 2004 | | |
| Burracoppin Rock | Merridan | 31 24 | 118 27 | 2004 | 2004 | | | |
| Yorkrakine Rock | Tammin | 31 25 | 117 30 | 2003/4 | 2003/4 | | | |
| Strawberry Rock | Southern Cross | 31 27 | 119 17 | 2003 | 2003 | | | |
| Merridan Rock | Merridan | 31 28 | 118 18 | 2004 | 2004 | | | |
| Jillbadgie Rock | Southern Cross | 31 29 | 119 14 | 2003/4 | 2003/4 | | | |
| Frog Rock | Southern Cross | 31 30 | 119 14 | 2003 | 2003 | | | |
| Dulyalbin Rock | Southern Cross | 31 34 | 118 59 | 2004 | 2004 | 2004 | | |
| Cave Hill Rock | Norseman | 31 39 | 121 14 | 2004 | 2004 | 2004 | | |
| Sunday Soak | Norseman | 31 43 | 121 27 | 2004 | 2004 | 2004 | | |
| Mt Hampton | Southern Cross | 31 45 | 119 04 | I. Bayly | I. Bayly | | | |
| near Madura | Nullabor Plain | 31 55 | 127 04 | | | | | *Lynceus* sp.- WAM |
| Cairn Rock | Narrembeen | 31 51 | 118 50 | | I. Bayly | | | |
| Coarin Rocks | Bruce Rock | 31 56 | 117 45 | | 2003 | | | |
| 25 Mile Rocks | Norseman | 31 57 | 121 37 | | 2003 | | | |
| McDermid Rock | Coolgardie | 32 02 | 120 43 | 2003/4 | 2003/4 | 2003/4 | | |
| Nutysland Nature Res. | Nullabor Plain | 32 03 | 126 06 | | | | | *Lynceus* sp.- WAM |
| Mt Walker | Narrembeen | 32 04 | 118 45 | 2004 | 2004 | | | |
| Buldania Rocks | Norseman | 32 04 | 122 02 | | 2003/4 | | 2003/4 | |
| Newmans Rocks | Norseman | 32 07 | 123 10 | 2003 | 2003 | 2003 | | |
| Disappointment Rock | Norseman | 32 08 | 120 56 | 2003/4 | 2003/4 | 2003 | | |
| Anderson Rocks | Hyden | 32 10 | 118 51 | 2003/4 | 2003/4 | 2004 | | |
| The Humps | Hyden | 32 17 | 118 57 | 2004 | 2004 | | 2004 | |
| King Rock | Hyden | 32 19 | 119 09 | 2004 | 2003/4 | 2003/4 | | |
| Corrigin Rock | Corrigin | 32 20 | 117 53 | | 2003 | | | |
| Afghan Rock | Balladonia | 32 21 | 123 40 | | 2003 | 2003 | | |
| Sullivan Rock | Armadale | 32 22 | 116 15 | | 2003 | | | |
| Bushfire Rks | Hyden | 32 26 | 119 20 | 2003/4 | 2003/4 | 2003 | | |
| Wave Rk | Hyden | 32 27 | 118 54 | 2003 | 2003/4 | | | |
| McPherson Rks | Norseman | 32 27 | 121 40 | 2003/4 | 2003/4 | 2004 | | |
| Graham Rocks | Hyden | 32 28 | 119 03 | 2004 | 2003/4 | 2003 | | |
| Emu Rock | Hyden | 32 28 | 119 25 | 2004 | 2003/4 | 2004 | | |
| Balladonia Rock | Balladonia | 32 28 | 123 52 | | 2003 | | | |
| Boyagin Rock | Brookton | 32 29 | 116 55 | | 2003 | | | |
| Moir Rock | Norseman | 32 39 | 121 25 | 2004 | 2003/4 | 2004 | | |
| Jilakin Rock | Kulin | 32 40 | 118 20 | | 2003 | | | |
| Sugg Rock | Lake King | 32 58 | 119 39 | 2004 | 2004 | 2004 | | |
| Dingo Rock | Lake Grace | 33 01 | 118 36 | | 2003 | | | |
| Lilian Stokes Rocks | Lake King | 33 04 | 120 06 | 2003 | 2004 | 2003 | | |
| Mt Madden | Lake King | 33 15 | 119 51 | 2003/4 | 2003/4 | 2004 | | |
| Mt Ridley | Esperance | 33 17 | 122 07 | | 2004 | 2004 | | |
| Puntipin Rock | Wagin | 33 20 | 117 24 | | 2003 | | | |
| Dunn Rock | Newdegate | 33 21 | 119 30 | | 2004 | | | |
| Holland Rocks | Newdegate | 33 22 | 118 45 | | 2003/4 | 2003 | 2003 | |
| Boyatup Hill | Esperance | 33 44 | 123 02 | | 2004 | 2004 | | |
| Peak Head | Albany | 35 07 | 117 56 | | D.Pirotta | | | |

* Years in these columns refers to dated collections made by the author